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THE MATERIAL BASIS OF MENDELIAN PHENOMENA ¹

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SINCE the rediscovery of Mendel's results at the beginning of the century, a very extensive and important field of hereditary phenomena has been actively developed, and the conceptions and explanations of Mendelian behavior have been changing with great rapidity. Many explanations and views of the phenomena of dominance, recessivity, latency and segregation have been proposed, and the only conception of Mendel which has remained essentially unmodified by Mendelians is that of the purity or unity of the characters in the gametes. Even this conception has been viewed by various workers in many lights, with a more or less complete and sweeping denial of an actual segregation of characters in the germ cells.

In the time at my disposal I shall bring before you the results of only one *Oenothera* cross, which shows Mendelian behavior in certain characters, and in the discussion of these results shall point out certain modifications of our conceptions of Mendelian segregation which they necessitate.

The cross in question is *Oenothera nanella* $\times$ *O. biennis*, *O. nanella* being a mutant from *O. Lamarckiana* and the *O. biennis* in the cross being from a wild race growing around the New York Botanical Garden. The seeds were first obtained from Dr. D. T. MacDougal. In the F_1 of this cross two types were produced, evidently corresponding to DeVries's twin hybrids. One of these types breeds true in the second generation and is the same as the type obtained in the F_1 of *O. Lamarckiana* $\times$ *O. biennis*. The other is a new type, with unexpected

¹ This paper was presented before the American Society of Naturalists in Boston, Mass., December 29, 1909.

characters, which I have called *O. rubricalyx*. None of the peculiar characters of either parent are present in this hybrid. But this is not so remarkable, because crosses between the *Oenothera* mutants frequently lose the distinctive marks of both parents and give *O. Lamarckiana*. The same form, *O. rubricalyx*, has appeared in my cultures as a mutant or extreme variant from *O. rubrinervis*, from which it differs only in possessing a red hypanthium instead of green, a marked increase in the red color pattern of the sepals (the median ridge of the sepals being also red instead of green), and in the production of a conspicuous quantity of red pigment on the *under* surface of the petioles of the rosette leaves, as well as in other parts of the plant. The type can therefore easily be recognized by observing the under surface of the rosettes, and in the flowering stage the conspicuous deep red buds render the plant very attractive and showy, distinguishable from *O. rubrinervis* at a glance. It differs from *O. rubrinervis* in its greatly increased capacity for anthocyanin production, a difference which expresses itself in nearly every organ of the plant. A full illustrated account of this cross will be published elsewhere.

In the F_2 this type splits in the Mendelian ratio of 3:1, giving approximately 75 per cent. *O. rubricalyx* and 25 per cent. *O. rubrinervis*. I have not yet bred the later generations, but the *O. rubrinervis* may be expected to breed true and the *O. rubricalyx* to split as before.

In this single cross there are many facts which throw interesting side lights on the nature of Mendelian behavior. In the first place, only one character splits in Mendelian fashion, the others remaining true. Hence, if proof of this proposition were needed, here we have proof that Mendelian phenomena are not universal, even in the forms in which they occur. The *O. rubricalyx* which appeared as a mutant from *O. rubrinervis* also splits in the same manner, a certain number of the offspring reverting to the *rubrinervis* condition, though I have not been able to determine whether this is a Mendelian ratio. These and other facts make it very prob-

able that the explanation of Mendelian phenomena is to be sought in the nature of the character itself, which conditions and perhaps determines this type of inheritance.

Another important point in connection with this hybrid is that the split in the F_2 does not produce a return to the condition of one of the grandparents, as in typical Mendelian behavior, but the difference between the two types of the F_2 —*O. rubricalyx* and *O. rubrinervis*—is a purely quantitative difference, in capacity for pigment production, although morphologically this difference is expressed in certain very definite regions of the plant. There are no intermediates between these two types, each being an independent condition of stability. The difference, therefore, clearly dates back to the germ cells.

That a quantitative difference between germ cells in their capacity for pigment production can behave in Mendelian fashion, showing the phenomena of dominance and segregation, is of fundamental significance in the interpretation of the nature and material basis of these phenomena.

Riddle ('09) has brought together in an interesting way the facts of physiology and biochemistry which show that the various pigment colors in mammals and other animals are different stages in the oxidation of a single melanin pigment by the enzyme tyrosinase. In the light of the facts of quantitative Mendelian inheritance which I have presented, it is clear that color inheritance in the mammals can also be most easily interpreted as a case of quantitative inheritance, due to initial quantitative differences of some sort in the germ cells themselves. It is not impossible that nearly all Mendelian inheritance may be found, on sufficient analysis of the characters, to be of this sort. Studies in variation show that many apparently qualitative differences, when analyzed, are found to be purely quantitative in origin. It should be remembered in the case of melanin pigments, as Riddle also points out, that while some tyrosin oxidations lead to the formation of melanins, others result in the usual

waste products, such as carbon dioxide and ammonia. Of course, only the former can be of significance in inheritance, and it is probable that whatever determines in how far the former process of tyrosin oxidation shall take place, will be found to control or determine these quantitative differences in the end-products of the germ cells.

It is interesting and suggestive to note in this connection that Morgan ('09) has adopted a quantitative interpretation of the sex-determining factors in the germ cells of insects and other organisms.

It is important to enquire what is the nature and origin of this quantitative difference, such as must occur in the germ cells of the hybrids I have described. It is most reasonable to suppose that it originates at the time the germ cells are formed, *i. e.*, during the reduction divisions, for the whole individual from a very early stage of the seedling to mature development shows one or the other of the alternative characters. Hence, the germinal difference must date back to the fertilized egg, and if this be true we must logically take it back farther still, on account of the definite Mendelian proportions, to the individual germ cells which united in fertilization, and hence probably to the reduction divisions.

The question of the relation of the chromosomes to Mendelian behavior has been so often discussed that I will only touch upon it here, to point out that the theory of qualitative hereditary differences among the chromosomes is not incompatible with the view that differential Mendelian characters are properties of the germ cell as a whole. If, during the reduction division, certain of the chromosomes which are segregated into separate cells are chemically unlike, then different groupings will arise and the whole germ cells whose nuclei the different groups enter will soon experience the effect of those differences, and accordingly such germ cells would be expected to become unlike as a whole. This follows necessarily, not only from the continual active inter-

changes in metabolism between nucleus and cytoplasm, but from the unity of the cell, which modern biology has abundantly proved. Hence there is no difficulty in supposing that differences which must be thought of as characterizing the germ cell as a whole, originated from chromosomal differences during reduction. On the other hand, there seems no necessity for assuming that *all* germinal differences originate in the chromosomes, although if they originated in the cytoplasm it is necessary to assume as a *vera causa* either a separation of cytoplasmic substances during reduction, of which we have no visible evidence, and which seems unlikely for various reasons, or *quantitative* cytoplasmic differences in the cells of a tetrad. The quantitative difference which must exist between the germ cells of *O. rubricalyx* and *O. rubrinervis* may possibly be conceived of as originating in the cytoplasm and then becoming a property of the germ cell as a whole.

It is even possible that this is not a difference in amount of matter of any sort, but rather in the energy-content of the two types of germ cell, although we have no means of knowing how or why such a marked difference in energy-content should arise.

To attempt to account for the manner of origin of a *O. rubricalyx* mutant from a *O. rubrinervis* germ cell would at the present time be purely speculation. DeVries' conception of a new unit becoming suddenly activated in the germ plasm seems too formal an assumption to be accorded the dignity of an explanation. The fact that the *O. rubricalyx* mutant reverts to *O. rubrinervis* may be looked upon as evidence in favor of his view that a mutant originates as a hybrid, from the union of a mutated with a non-mutated germ cell.

I should also point out that the origin of *O. rubricalyx* from *O. rubrinervis* may perhaps be significant as indicating an orthogenetic tendency to an increase of pigment production, although this increase has taken place by definite germinal steps, particularly in the origin of *O. rubricalyx* from *O. rubrinervis*.

The significance of the fact that I have succeeded in producing *O. rubrinervis* as one of the types resulting from this cross, is too obvious to require pointing out. In the light of these facts, it is not impossible that other mutants can be similarly synthesized.

Much experimental work has been directed to the study of the physiology of anthocyanin production in the plant. Without entering into the details of this work it may be said that two general theories of anthocyanin production have been developed. E. Overton ('99), Mirande ('07), Molliard ('07) and others conclude that it arises from an accumulation of sugars in the cell sap, which unite with tannic acid to produce a glucoside. Overton showed experimentally that low temperature and high light intensity both cause anthocyan production. Mirande ('07) called attention to the development of red in leaves eaten by insects;² and Combes ('09a) produces the same result by annular decortication. In every case the result is interpreted as due to an accumulation of sugars. J. Laborde ('08), from his experiments deduced a slightly different view, namely that formaldehyde or one of its polymerization products may cause tannin transformation, to produce color. Further, Overton, Laurent, Molliard and others, found that various seed plants grown in sugar solution show a marked increase in anthocyan production, which indicated clearly a relation, direct or indirect, between the presence of sugars and the development of anthocyan. Whether such an increase in anthocyan production is inherited is not known, but presumably it would not be inherited. Of course, many variations in pigment production are of a non-heritable sort, but it is equally certain that in *O. rubri-*

² In this connection I may call attention to certain observations of my own upon the effects of the attacks of a certain insect on the buds of *Oenothera*. The very young buds are stung by this insect and such buds undergo several characteristic changes in development. The hypanthium fails to develop and the base of the cone becomes very thick. In *O. Lamarckiana* (and the same is true at least of several mutants) there is also always a conspicuous amount of red developed on the sepals under these circumstances, but the buds of *O. biennis*, while they undergo the same morphological changes, never develop any red.

calyx the increased pigment production is a heritable character, and therefore the change which brought it about must have been of a fundamental sort, in the germ plasm.

A more recently developed hypothesis of anthocyan formation, suggested by Pick in 1883 and supported by the work of Palladin ('08), Buscalioni and Pollacci ('04), in their extensive memoir, and others, is that anthocyan originates from the action of oxydases upon the respiratory chromogens of the cell, the latter being aromatic bodies which on oxidation yield colored compounds. The experiments of Molliard ('09) support the latter theory by showing the necessity for the presence of oxygen in anthocyan production. Molliard also showed that, when grown in a sugar solution, the respiratory exchanges of plants are more intense.

Combes ('09*b*) has recently harmonized the two theories. He shows that there is a close relation between the production of anthocyan and an increase in the proportion of sugars and glucosides in the cell sap. He concludes that since the formation of anthocyan, a compound of glucoside nature, is correlative with an increase of the total glucosides, the anthocyan cannot be formed from preexistent glucosides, but from some other source; and since there is also an increase in chromogens (Palladin) therefore anthocyan is not derived from chromogens already existing, but its formation must be provoked by the accumulation of sugars, which increases the respiratory exchanges and appears to determine the acceleration of oxidation processes. Under these conditions the production of glucosides is increased, and these are, in part at least, anthocyanins.¹

It is scarcely necessary to point out that, whatever may be the chemistry and physiology of anthocyanin production, in the case of *Oenothera rubricalyx* there must have been a fundamental change in the germ plasm by reason of which, under the same external conditions as *O. rubri-*

¹ See also the important recent papers of Miss M. Wheldale. Proc. Roy. Soc. London B, 81: 41-60. Proc. Cambridge Phil. Soc. 15: 137-168 and Reports to the Evolution Committee of the Royal Society, V., pp. 26-31, 1909.

nervis, it reacts with much greater pigment production; a reaction which shows itself with great definiteness in the buds and the rosette leaves.

Although plants and animals equally exhibit Mendelian phenomena, yet the part of the organism which must be looked upon as constituting the germ plasm, and hence the basis of such phenomena, shows several important differences in Metazoa and Metaphyta, two of which may be pointed out. Most important of these differences is probably the absence of a *Keimbahn* in plants, in the sense in which it is known to be present in many animals. The classical cases of *Ascaris* (Boveri) and *Cyclops* (Häcker) need only be cited. More recently, other work, such as that of Hegner ('09) in the Coleoptera, has shown that the germ cells are formed from certain free nuclei, at an early stage in the segmentation of the egg. Thus set aside, they rest and undergo very few divisions, until a late stage of embryonic life. There is no evidence whatever of a similar process in higher plants, and it is probably made impossible by the method of plant growth. On the other hand, it may be pointed out that while, in plants, there are no resting cells set aside in the body tissues, to serve later as reproductive cells, yet a lineage of cells exists, which may be looked upon as a *Keimbahn* in one sense. Every one who has studied plant embryos recognizes their characteristically large nuclei with huge nucleoli having a large chromatin content. A similar appearance is characteristic of all undifferentiated meristematic cells, so that such cells, forming a lineage from the egg cell to the spore mother cells, may be thought of as constituting a *Keimbahn* for the plant, though evidently in a somewhat different sense from that in which the term is employed for animals. The fact that in such a lineage, a great number of cell generations intervene between the fertilized egg and the spore mother cell, together with the fact that the meristematic cells forming this lineage are near the surface of the plant, where they are almost directly exposed to environmental influences (and not hidden away in the in-

terior of the body as in animals), doubtless accounts for the greater plasticity exhibited by plants. Indeed, it is a matter for wonder that, under these conditions, plants show such hereditary constancy. The accurate reproduction, generation after generation, of the most minute hereditary differences, shows the relative fixity of the material of the germ plasm.

The work of the Marchals ('06 and '07) with the mosses seems to show clearly that, during the meiotic divisions of spore formation, an actual segregation of sex-producing tendencies or elements takes place. Much other evidence of a similar sort in plants might be cited if time permitted, and the case of the sex chromosomes in insects is too well known to require more than mention. But while the reduction divisions seem the most natural place to look for an explanation of the Mendelian proportions, yet on the other hand there is much evidence that the phenomena of "splitting" also occur at other times in the life history. Bateson ('05) has shown that in two races of sweet peas (*Lathyrus odoratus*), one of which has long pollen grains and the other round, the long pollen character is dominant in the F_1 . If a segregation of characters took place here during the reduction divisions, we should find 50 per cent. of each type of pollen grain. But plants having long pollen give only long, or they may give three plants with long pollen to one with round. Only in "very rare and exceptional" cases is there a mixture of long and round in the same plant, and in such cases they are found only in certain flowers of an individual. Rosenberg ('06) found that in the hybrid *Drosera longifolia* $\times$ *D. rotundifolia*, in some cases two pollen grains of a tetrad resemble each parent, the grains differing chiefly in size. More recently, however, he has found ('09) that the variations in the size of the hybrid pollen grains probably depend upon the numbers of chromosomes which enter the respective daughter nuclei during reduction, and hence this difference in pollen grains will no longer serve as evidence for a segregation of characters at this time.

There is nothing to indicate that the phenomena of

vegetative splitting, or reversion to the parental types, in such forms as the reputed graft-hybrid, *Cytisus Adami*, differ in any essential respect from Mendelian segregation in germ cells. In angiosperms, the great majority of which are hermaphrodite, there is a separation of tendencies, which may be thought of as a "segregation," in the Anlage of every flower, the stamens producing microspores and male gametophytes, while the ovules bear the megaspores, which develop the female gametophyte. These two tendencies—namely, for the stamens to produce microspores and the ovules to produce the female gametophyte—are almost never interchanged (although Němec, '98, has described a case in *Hyacinthus*, in which the microspores may produce a structure resembling more or less the female gametophyte). Whether there is here a separation of substances in the cytoplasm or chromoplasm during the division of certain cells in the Anlage of the flower, is not known, but it is not impossible that such is the case.

Viewed from this standpoint, all differentiation during ontogeny may be considered a "segregation." A consideration of what this really consists in would involve the whole great problem of individual development, which I shall not touch upon here. But it may be pointed out that maturation, particularly in Mendelian hybrids, may be looked upon as a period of active germ cell differentiation.

The factors involved in such differentiation may be, in some cases, quite as complex as those involved in development itself, but as I have shown from the evidence of these *Oenothera* hybrids, and as appears from color inheritance in mammals and from other evidence, in many cases at least the difference between Mendelian germ cells must be of a simple quantitative sort, involving either a difference in the amount of certain material substances or a difference in the energy-content of certain constituents.

From this point of view, many instances of Mendelian behavior are seen to be cases of quantitative inheritance.

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